Selaginella pseudotamariscina (Selaginellaceae), an overlooked rosette-forming resurrection spikemoss from Vietnam

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Abstract: A new species, *Selaginella pseudotamariscina* (Selaginellaceae), is described from Vietnam. The placement of this species within *Selaginella* subg. *Stachygynandrum* is assessed based on a molecular phylogenetic analysis and morphological comparisons with related species. Molecular phylogenetic analyses suggested that *S. pseudotamariscina* is sister to *S. digitata-S. imbricata* clade. Morphologically, the new species is similar to *S. tamariscina* and *S. pulvinata* by sharing the rosette-forming habit, but distinguished by its dorsal leaves symmetrical, lanceate, sulcate on upper surface; strobili slightly dorsiventrally complanate and non-resupinate, sporophylls resembling vegetative leaves in form and arrangement, non-resupinate, the ventral sporophylls larger than the dorsal ones, dorsal sporophylls sterile, sporangia only borne on the base of ventral sporophylls.

Keywords: chloroplast gene *rbcL*, resurrection plants, *Selaginella* subg. *Stachygynandrum*

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越南莲座状复苏卷柏一新种——越南卷柏（卷柏科）

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摘要：该文描述了在越南发现的卷柏科一新种——越南卷柏 (*Selaginella pseudotamariscina* X.C. Zhang & C.W. Chen)。基于叶绿体基因片段 *rbcL* 构建的系统发育关系结果表明该新种是卷柏属 (*Selaginella*) 同穗亚属 (subg. *Stachygynandrum*)的一个物种，与 *S. digitata-S. imbricata* 分支为姐妹群关系。该新种与卷柏 (*S. tamariscina*) 和垫状卷柏 (*S. pulvinata*) 的形态近似，它们植株都为莲座状，其不同之处在于中叶对称，似披针形，上表面具 1 沟槽；孢子叶穗略压扁；孢子叶和营养叶性状和排列近似，孢子叶非同形，略异形，正置，腹面孢子叶大于背面孢子叶；背面孢子叶败育，孢子囊仅见于腹面孢子叶基部。

关键词：叶绿体基因 *rbcL*，复苏植物，卷柏属同穗亚属

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1 Introduction

Selaginella P. Beauv. (1804) is the single genus of Selaginellaceae. It is the largest genus of lycophytes, containing ca. 700-800 species, widely distributed throughout the world, with the greatest diversity in the tropics and subtropics (Jermy, 1990; Weststrand & Korall, 2016a,b; Zhang et al., 2020). Several morphology-based classifications were proposed (Spring, 1840, 1850; Baker, 1883; Hieronymus & Sadebeck, 1902; Walton & Alston, 1938; Jermy, 1986). Based on the most recent molecular phylogenetic studies seven subgenera were recognized within the *Selaginella*: subg. *Ericetorum* Jermy, subg. *Exaltatae* Weststrand & Korall, subg. *Gymnogynum* (P. Beauv.) Weststrand & Korall, subg. *Lepidophyllae* (Li Bing Zhang and X. M. Zhou) Weststrand & Korall, subg. *Rupestrae* Weststrand & Korall, subg. *Selaginella*, and subg. *Stachygynandrum* (P. Beauv. ex Mirb.) Baker (Weststrand & Korall, 2016a, b; Zhang et al., 2020).

Selaginella is morphologically characterized by possessing rhizophores, heterospory, leaves generally arranged in four decussate rows, and terminal strobilus. Species of this genus have various growth forms, including climbing, creeping, prostrate, erect, suberect, and rosette forms (Jermy, 1990; Zhang, 2004; Zhang et al., 2013). Rosettes is a rare morphological feature in *Selaginella* (occurring in ca. 1% species). Only a few members of subg. *Lepidophyllae* and *subg. Stachygynandrum* are rosettes which are all resurrection plants (Weststrand & Korall, 2016a).

Recently, Mr. Cheng-Wei Chen kindly shared us a new specimen (*Wade 5314*) collected from the southern central coast of Vietnam. It is different from *S. tamariscina* (P. Beauv.) Spring and *S. pulvinata* (Hook. & Grev.) Maxim. by its dorsiventrally complanate strobilus (vs tetragonal strobilus) and symmetrical lanceate dorsal leaves. Historical collections from Vietnam of this species were all identified as *Selaginella tamariscina* (Alston, 1951). In order to correctly identify the specimen and infer the phylogenetic position of this unknown species, we analyzed the sequence of the chloroplast gene *rbcL* of it together with representatives of different subgenera of *Selaginella* with special attention to the rosettes plants. Both morphological and phylogenetic studies suggested that it represents an undescribed species. We therefore described it as a new species named *Selaginella pseudotamariscina* X.C. Zhang & C.W. Chen and presented the results here.

2 Materials and Methods

2.1 Morphological assessment Morphology of the newly collected specimens was examined and compared to that of *Selaginella tamariscina* and *S. pulvinata* using specimens from the herbarium of Institute of Botany, CAS (PE). Sterile leaves, strobili, and sporophylls were observed and photographed under a Leica S9D stereo microscope.

2.2 Molecular analyses In total, 32 individuals were sampled to represent 7 subgenera of *Selaginella*, with *Isoetes flaccida* as the outgroup. Sequences were obtained from the GenBank except for the new species (Voucher information and GenBank accession numbers are provided in the Table 1). Phylogenetic reconstruction was based on the chloroplast gene *rbcL*. We extracted total genomic DNA from silica gel dried materials using a modified cetyl trimethylammonium bromide (CTAB) method (Li et al., 2013). Library construction was performed with the NEBNext DNA Library Prep Kit (New England Biolabs, Ipswich, Massachusetts, USA). Paired-end reads of 2 × 150 bp were generated on an Illumina HiSeq 2500 instrument, and *rbcL* gene was extracted.

Sequences were aligned using MUSCLE (Edgar, 2004), followed by manual adjustment in

PhyDE v0.9971 (Muller et al., 2010). Maximum likelihood (ML) analyses were performed using RAxML 7.2.6 (Stamatakis, 2006), with 1 000 bootstrap replicates under the GTRGAMMA model. We performed Bayesian inference (BI) analyses in MrBayes v. 3.2.6. (Ronquist et al., 2012) under the GTR + G + I model. For each Bayesian analysis, four MCMC chains were run simultaneously for 2 million generations, and sampled every 1 000 generations. The average standard deviation of split frequencies (< 0.01) was used to assess the convergence. ML and BI trees and the branch support values were visualized using FigTree v.1.4.2 (Rambaut, 2014).

Table 1 Species names and GenBank accession numbers of DNA sequences used in this study

Taxon	**Locality**	**Voucher specimen**	***rbcL***
Isoetes flaccida Shuttlew. ex A. Braun	–	*Abbott 20265* (FLAS)	KJ773600
Selaginella braunii Baker	Cult, Thailand	*Tiew 12* (CDBI)	KT161421
S. bryopteris (L.) Baker	Nepal	*C. R. Fraser-Jenkins 4370* (L)	KY022983
S. ciliaris Spring	Yunnan, China	*X. C. Zhang 7780* (PE)	MH814892
S. convoluta (Arn.) Spring	Bahia, Brazil	*R. M. Harley 16181* (U)	KY023003
S. digitata Spring	Madagascar	*N. Wikstr öm et al. 110319-2* (S)	KY023013
S. digitata Spring	Madagascar	*P. Phillipson 1826* (L)	KY023012
S. exaltata (Kunze) Spring	Ecuador	*Korall 1996-1* (S)	AJ010849
S. helicoclada Alston	–	*Rakotondrainibe 3262* (P)	AJ295896C
S. helvetica (L.) Spring	France	*J. C. Bertier 9161* (PE)	MW407303
S. heterostachys Baker	Guizhou, China	*X. C. Zhang 7088* (PE)	MH814896
S. imbricata (Forssk.) Spring	Dhofar Governorate, Oman	*Rothfels et al. 4275* (DUKE)	KT161486
S. kraussiana (Kunze) A. Braun	Democratic Republic of the Congo (South Kivu)	*M. Mokoso 3098* (BR)	KY023057
S. lepidophylla (Hook. & Grev.) Spring	–	–	AF419051
S. lutchuensis Koidz.	Japan	*TNS759343* (TNS)	AB574648
S. moellendorffii Hieron.	Sichuan, China	*Ju & Deng HGX12295* (CDBI)	KT161531
S. nipponica Franch. et Sav.	Guizhou, China	*X. C. Zhang et al. 7066* (PE)	MW407367
S. nothohybrida Valdespino	San Luis Potos í, Mexico	*C. J. Rothfels 3069* (DUKE)	KY023096
S. novoleonensis Hieron. & Sadeb	Sonora, Mexico	*F. Drouet and D. Richards 3942* (S)	KY023097
S. nubigena J. P. Roux	South Africa	*A. Larsson AL810* (UPS)	KY023098
S. *pallescens* (C. Presl) Spring	Unknown	–	AJ295859
S. pilifera A. Braun	–	*Pringle 13959* (S)	AJ295862
S. pseudotamariscina X.C. Zhang & C.W. Chen, sp. nov.	Vietnam	*C. W. Chen Wade 5314* (PE)	MZ159980*
S. pulvinata (Hook. & Grev.) Maxim	Sichuan, China	*D. E. Boufford et al. 37879* (A)	KY023124
S. pulvinata (Hook. & Grev.) Maxim	Yunnan, China	*D. E. Boufford et al. 35254* (A)	KY023125
S. remotifolia Spring	Yunnan, China	*Gaoligong Shan Biodiversity*	KY023130

		Survey 21081 (GH)	
S. selaginoides (L.) P. Beauv. ex Schrank & Mart.	Sweden	*S. Weststrand 104* (UPS)	KY023148
S. sibirica (Milde) Hieron.	–	*Alaska L. A. Viereck and K. Jones 5667* (S)	KY023153
S. stauntoniana Spring	Beijing, China	*Zhao 169* (CDBI)	KT161614
S. tamariscina (P. Beauv.) Spring	Japan	*TNS759348* (TNS)	AB574655
S. uliginosa (Labill.) Spring	–	*Holmgren and Wanntorp 253* (S)	AJ010843
S. uncinata (Desv.) Spring	Sichuan, China	*Zhang and Zhou DJY04101* (CDBI)	KT161626
S. vardei H. Lév.	Tibet	*D. E. Boufford et al. 32425* (A)	KY023169

Note: A dash (–) indicates missing data; An asterisk (*) indicates newly generated sequences.

3 Results and Discussion

The ML and BI topologies are totally identical, and the BI tree is shown in Fig. 1. The results of the molecular phylogenetic analyses showed that the new species nested within subg. *Stachygynandrum*, forming sister relationships with the *S. pilifera-S. imbricata* clade with weak support (PP=0.56/ML=55). However, of species nested in the *S. pilifera-S. imbricata* clade, *S. pilifera* from America is the only rosette-forming species. The *S. pilifera-S. pseudotamariscina* clade was resolved to be sister to the *S. tamariscina-S. stauntoniana* clade with strong support (PP=1.0/ML=100). Morphologically, the new species is similar to *S. tamariscina* and *S. pulvinata*. However, the new species differs obviously in several features, such as the slightly anisosporophylls which are similar to sterile leaves in form and arrangement; dorsal leaves symmetrical, lanceate, and sulcate on upper surface; ventral leaves shallowly sulcate on upper surface with their basiscopic margins ciliolate or denticulate; sporangia borne only on ventral side of strobilus axes [Fig. 2, Fig. 3 (A1–B1), Table 2].

4 Taxonomic Treatment

***Selaginella pseudotamariscina* X.C. Zhang & C.W. Chen, sp. nov.** (Fig. 2).

Type: VIETNAM. Khanh Hoa Province, Orchid Island, on granite rocks, in coastal open forest, 22 September 2018, *Cheng-Wei Chen Wade 5314* (holotype, SGN!; isotypes, PE!, SING!, TAIF!).

Diagnosis: The new species is similar to *S. tamariscina* and *S. pulvinata* in the rosette-forming habits, differs by its slightly anisosporophyllous which are similar to sterile leaves in form and arrangement, dorsal leaves symmetrical, lanceate, and sulcate on upper surface, ventral leaves shallowly sulcate on upper surface with their basiscopic margins ciliolate or denticulate, and only the ventral sporophylls fertile.

Description: Rosettes, xerophytic. Rhizophores restricted to basal portions of stems forming thick massive rootstocks; stems and roots entangled forming treelike trunk. Primary leafy branchlets 2-3 pinnately branched, branchlets compact and regularly arranged. Leaves thick, surfaces smooth. Axillary leaves on branches symmetrical, lanceate, or ovate-lanceate, ca. 2.18 × 0.73 mm, with membranous margins which measure ca. 1/2 of the width from margin to leaf midvein, lacerate or subentire, bases obtuse, and ciliolate, apice short aristate (ca. 0.02 mm long). Dorsal leaves

strongly ascending, symmetrical, lanceate, 2.0–2.5 × 0.6–0.7 mm, sulcate on upper surface, carinate, bases obtuse, margins ciliolate or denticulate, slightly membranous, apices aristate (ca. 0.02 mm long). Ventral leaves slightly spreading, asymmetrical, ovate-lanceate to ovate-triangular, ca. 2.18 × 0.82 mm, shallowly sulcate on upper surface, apices aristate (ca. 0.04 mm long), basiscopic margins ciliolate or denticulate, acroscopic bases enlarged, broader than basiscopic, margins and becoming membranous outside, lacerate or subentire, ciliolate or lacerate proximally. Strobili solitary, terminal, compact, slightly dorsiventrally complanate, ca. 6 mm long; sporophylls similar to sterile leaves in form and arrangement, slightly anisophyllous; dorsal sporophylls smaller than ventral ones, lanceate-triangular, ca. 1.95 × 0.75 mm, margins ciliolate, slightly membranous, apices aristate (ca. 0.02 mm); ventral sporophylls triangular, ca. 2.13 × 0.98 mm, margins denticulate, ciliolate or lacerate, membranous, apices aristate (ca. 0.04 mm); only the ventral sporophylls fertile.

Additional specimens examined: VIETNAM. Khanh Hoa Province, Nhatrang, Cau da, 100 m, 27 February 1922, *Poilane 2651* (P01244600, image online!; US01393274, image online!; VNM00021481!, VNM00021483!, VNM00021486!); Khanh Hoa Province, Nhatrang, 50 m, 10 September 1922, *Poilane 4529* (VNM00021477!, VNM00021479!, VNM00021482!); Khanh Hoa Province, Nhatrang, Nui Hon Heo, 3 May 1923, *Poilane 6173* (VNM00021478!); Ninh Thuan Province, Phan Rang, 27 February 1924, *Poilane 9768* (MICH1173518, image online!; VNM00021475!); Ninh Thuan Province, Phan Rang, 350 m, 3 March 1923, *Poilane 5541* (MICH1173519, image online!; VNM00021480!); Ninh Thuan Province, Phan Rang, 200 m, 6 March 1923, *Poilane 5616* (P01244598, image online!; VNM00021484!).

Distribution and habitat: *Selaginella pseudotamariscina* is only known in Khanh Hoa and Ninh Thuan Provinces of southern central Vietnam (Fig. 4), growing on granite rocks in open coastal forests.

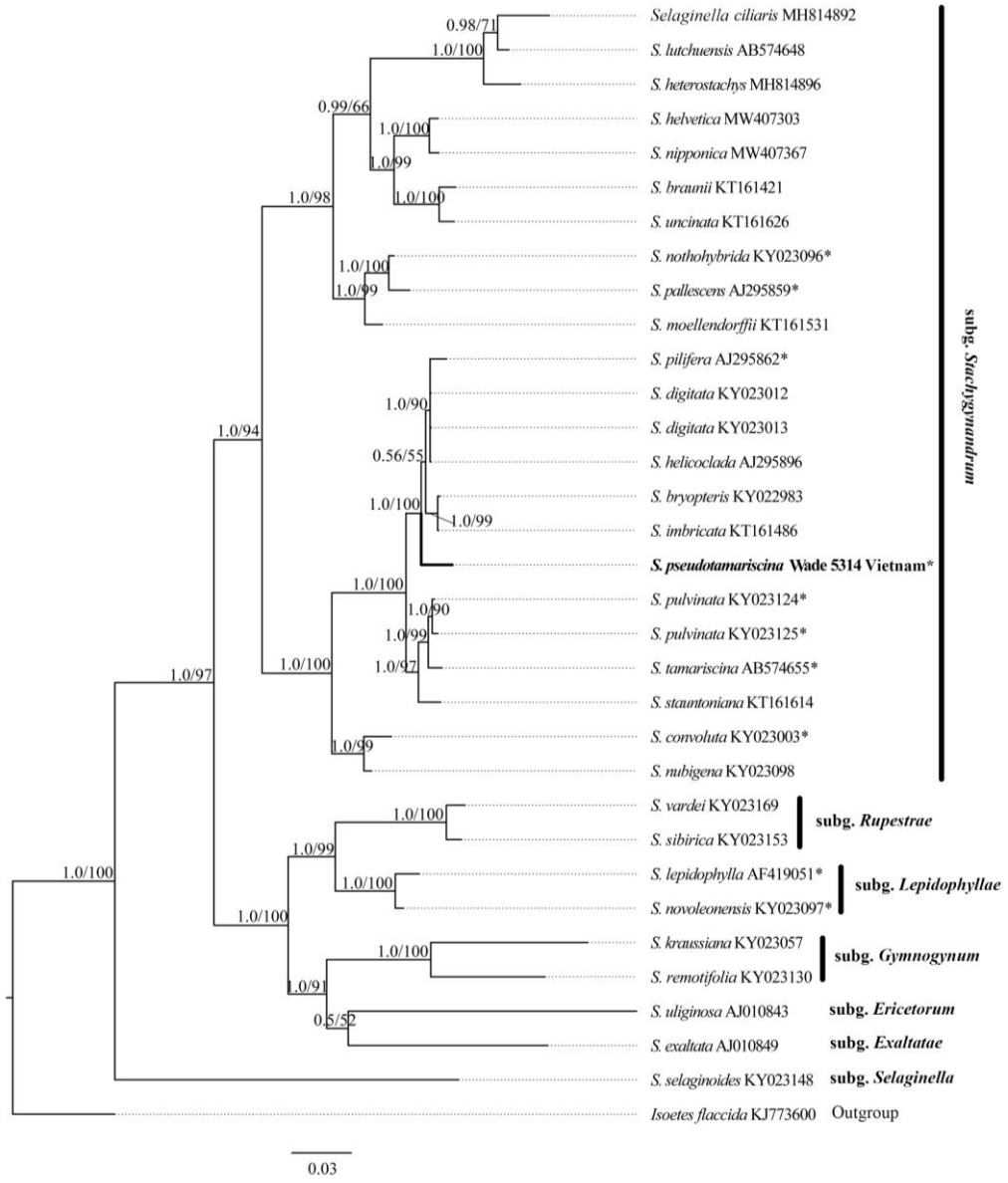
Etymology: The specific epithet '*pseudotamariscina*' refers to its close relation and morphological similarity with *S. tamariscina*.

Conservation status (EN): *Selaginella pseudotamariscina* is distributed only in two provinces in southern central Vietnam (Khanh Hoa and Ninh Thuan). There exist a few specimens of *S. pseudotamariscina* deposited in various herbaria and one of the oldest specimens was collected a century ago by the French collector E. Poilane in Nhatrang, which is preserved in herbarium P with a duplicate in the US. This rosette-forming species appears to have adapted to the coastal climate on granite rocks in southern central Vietnam. Here it is tentatively listed as an endangered (EN) species according to IUCN categories and criteria (IUCN, 2018).

Table 2 Comparison of morphological characters of *Selaginella pseudotamariscina*, *S. pulvinata*, and *S. tamariscina*

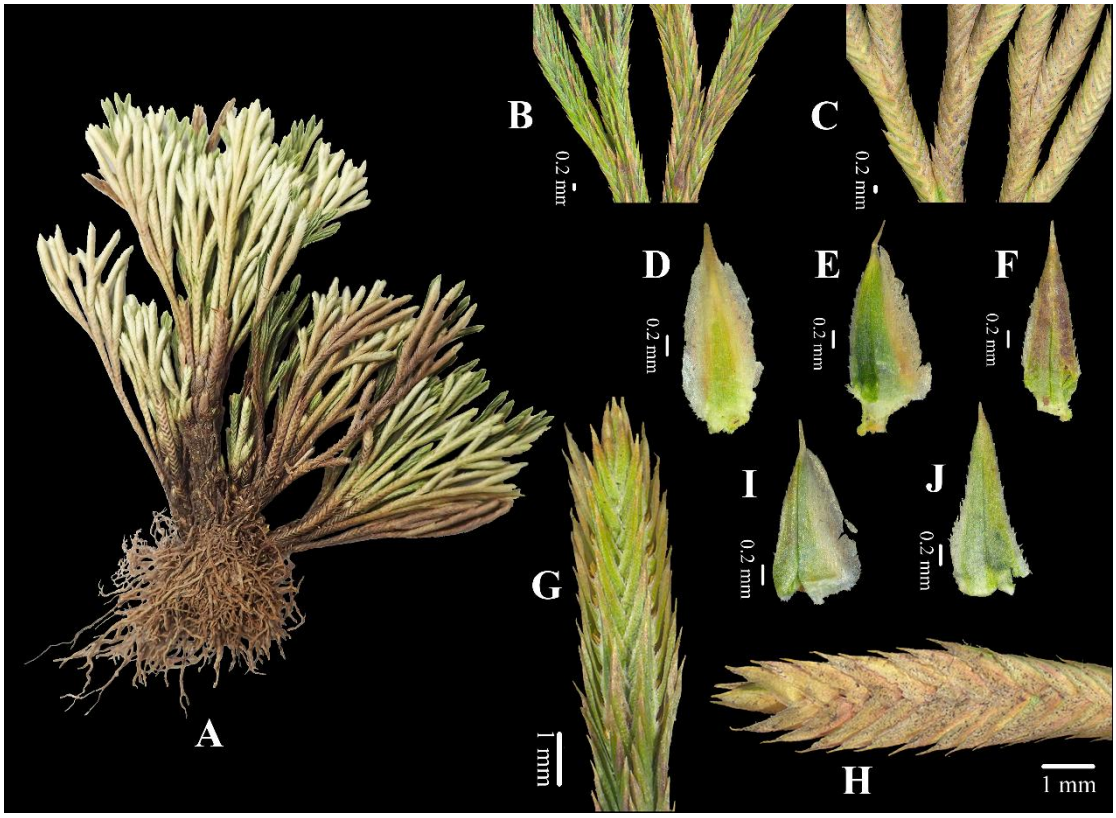
Characters/Species	*S. pseudotamariscina*	*S. pulvinata*	*S. tamariscina*
Stems	Forming treelike trunk	Not forming treelike trunk	Forming treelike trunk
Axillary leaves on branches	Lanceate, or ovate- lanceate, ca. 2.18 ×0.73 mm, margin lacerate-ciliolate	Ovate to triangular, ca. 2.5 ×1 mm, margin lacerate-ciliolate	Ovate, ovate-triangular, or elliptic, 0.8–2.6 ×0.4–1.3 mm, margin denticulate
Dorsal leaves on branches	Symmetrical, lanceate, 2.0–2.5 × 0.6–0.7 mm, sulcate on upper surface, margin ciliolate or	Asymmetrical, obliquely ovate or triangular, 2.8–3.1 × 0.9–1.2 mm, upper surface	Asymmetrical, elliptic, 1.5–2.5× 0.3–0.9 mm, upper surface without sulcate, margin

	denticulate	without sulcate, margin lacerate	denticulate (shortly ciliolate at base)
Ventral leaves	Ovate- lanceate to ovate-triangular, ca. 2.18 ×0.82 mm, shallowly sulcate on upper surface; basiscopic margin ciliolate or denticulate; acroscopic margin lacerate or subentire	Oblong, 2.9–3.2 ×1.4–1.5 mm, upper surface withoutsulcate; basiscopic margin and acroscopic margin lacerate	Ovate to triangular or oblong-ovate, 1.5–2.5 ×0.5–1.2 mm, upper surface without sulcate; basiscopic margin subentire, serrate or ciliolate (at base); acroscopic margin lacerate or denticulate
Strobili	Slightly dorsiventrally complanate	Tetragonal	Tetragonal
Sporophylls	Slightly anisophyllous; ventral sporophylls fertile, dorsal sporophylls sterile	Isophyllous; ventral and dorsal sporophylls both fertile	Isophyllous; ventral and dorsal sporophylls both fertile



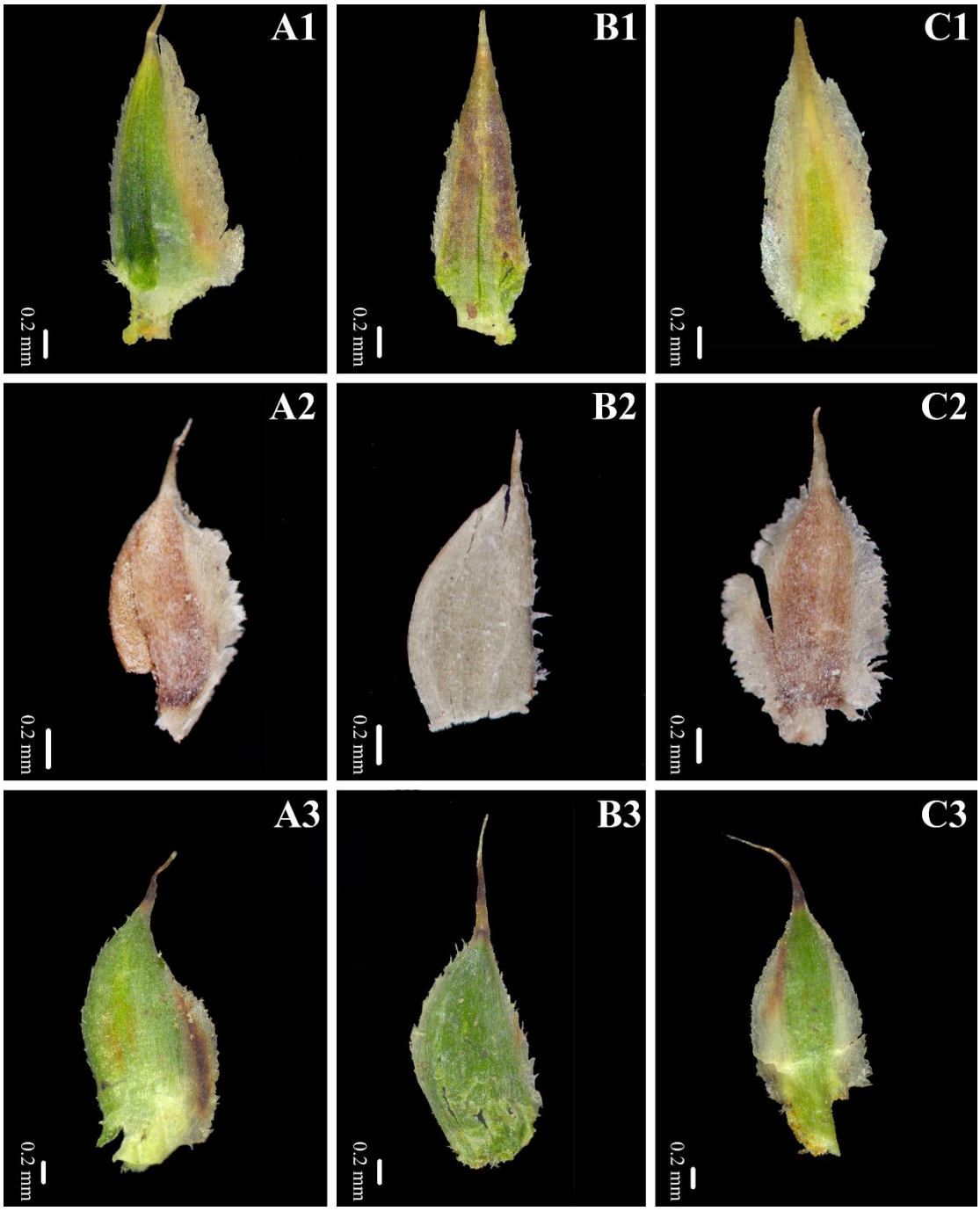
Bayesian inference posterior probability (PP) and maximum likelihood bootstrap (ML) are noted on the branches, respectively; The new species is shown in bold. An asterisk (*) indicates rosette forming.

Fig.1 Bayesian inference tree of the *Selaginella pseudotamariscina* and related species based on the *rbcL* gene



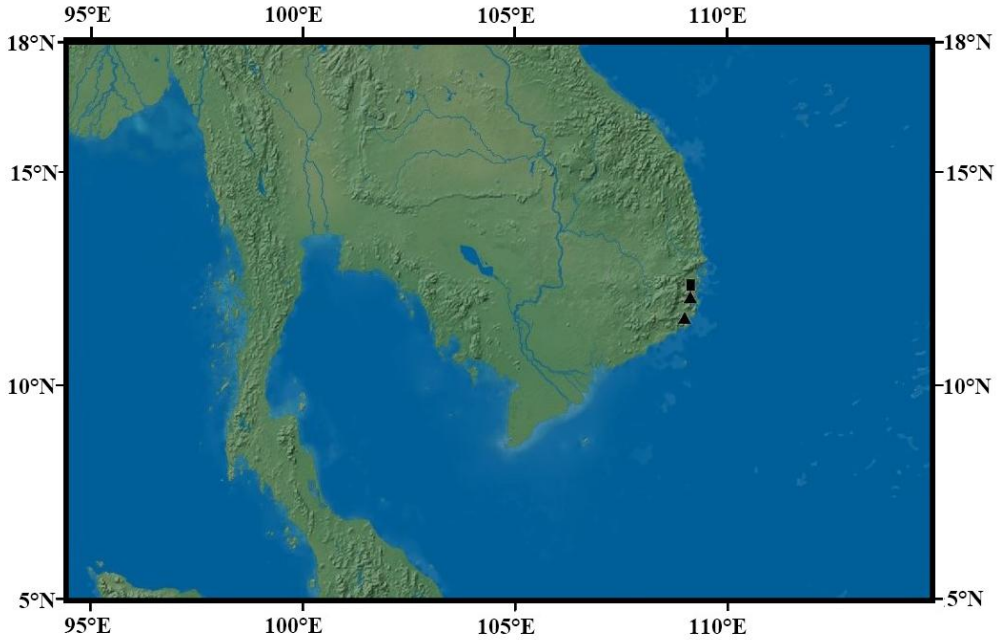
A. Individual; **B**. Upper view of branchlets; **C**. Lower view of branchlets; **D**. Axillary leaf (lower view); **E**. Ventral leaf (lower view); **F**. Dorsal leaf (upper view); **G**. Upper view of strobilus; **H**. Lower view of strobilus; **I**. Ventral sporophyll (lower view); **J**. Dorsal sporophyll (upper view).

Fig. 2 *Selaginella pseudotamariscina* X.C. Zhang & C.W. Chen, sp. nov., *Cheng-Wei Chen Wade 5314* (PE)



A1–C1. *Selaginella pseudotamariscina* (Vietnam, *C. W. Chen Wade 5314*, PE); **A2–C2**. *S. pulvinata* (China, Shanxi, *Yellow River Exped. 251*, PE); **A3–C3**. *S. tamariscina* (China, Fujian, *X. C. Zhang et al. 9634*, PE). **A**. Ventral leaves; **B**. Dorsal leaves; **C**. Axillary leaves.

Fig. 3 Comparison of leaf morphology of *Selaginella pseudotamariscina*, *S. pulvinata*, and *S. tamariscina*



The rectangle represents the type location of *S. pseudotamariscina*.

Fig.4 Distribution of *Selaginella pseudotamariscina* X.C. Zhang & C.W. Chen, sp. nov.

Key to *Selaginella pseudotamariscina*, *S. tamariscina* and *S. pulvinata*

1. Strobilus dorsoventrally complanate; ventral sporophylls fertile, dorsal sporophylls sterile; dorsal leaves symmetrical, lanceate, sulcate on the upper surface; ventral leaves shallowly sulcate on the upper surface…….... S. *pseudotamariscina* X.C. Zhang & C.W. Chen
1. Strobilus tetragonal; ventral and dorsal sporophylls both fertile; dorsal leaves asymmetrical, obliquely ovate, triangular, or elliptic, upper surface without sulcate; ventral leaves upper surface without sulcate……...…… 2
2. Stems and roots entangled not forming treelike trunk; inner margins of dorsal leaves lacerate or entire, outer margin revolute and entire…….…….… *S. pulvinata* (Hook. & Grev.) Maxim.
2. Stems and roots entangled often forming treelike trunk; inner margins of dorsal leaves denticulate, outer margin denticulate or shortly ciliolate…...… *S. tamariscina* (P. Beauv.) Spring

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